

How does Soil Respond to Wild-Type Endophyte Infection?

Alan J. Franzluebbers¹, Nicholas S. Hill², Michael B. Jenkins¹, David A. Zuberer³,
Shaheen B. Humayoun¹, and John A. Stuedemann¹

¹USDA Agricultural Research Service, 1420 Experiment Station Road, Watkinsville GA 30677

²University of Georgia, Department of Crop and Soil Sciences, Athens GA 30602

³Texas A&M University, Department of Soil and Crop Sciences, College Station TX 77843

Introduction

Toxic effects of *Neotyphodium*-infected tall fescue on grazing animals have been well documented (Stuedemann and Hoveland, 1988). Ecologically, the presence of *N. coenophialum* may be important for improved tall fescue persistence in marginal ecoregions (Bouton et al., 1993) by (1) conferring greater drought tolerance (West et al., 1993), (2) producing ergot alkaloids that reduce forage intake and subsequent grazing pressure (Hoveland et al., 1983), and (3) deterring insect and disease pressures (Clay, 1993).

Pastures with high occurrence of endophyte-infected tall fescue have also been found with greater soil organic C and N concentration (Franzluebbers et al., 1999). The magnitude of change in soil organic C (1.8 Mg Aha⁻¹) that was observed under high- versus low-endophyte infection suggests that if this difference were realized on the 14 Mha of tall fescue in the USA (Buckner et al., 1979), there is the potential to sequester 25 Tg of soil organic C due to endophyte infection of tall fescue alone. This change in soil organic C would be in addition to an estimate of 112 Tg of soil organic C that would be sequestered due to planting of tall fescue compared with conventional-tillage cropping.

We hypothesized that either (1) greater tall fescue growth and/or (2) reduced soil microbial activity might be causing organic C to accumulate to a greater extent in soil under tall fescue with high endophyte infection. To ascertain possible mechanisms that control soil organic C with endophyte infection, we conducted a short-term growth study, a short-term decomposition study, and sampled a long-term field study.

Methods

All experiments were carried out at the J. Phil Campbell Sr. Natural Resource Conservation Center in Watkinsville GA. The long-term field study consisted of 18, 0.7-ha paddocks planted in 1982 and sampled in 2002. Six treatments (K-31 tall fescue with low endophyte infection fertilized at low and high rates annually, K-31 tall fescue with high endophyte infection fertilized at low and high rates, and Johnstone and Triumph fertilized at a low rate) were replicated three times in a randomized block design. Soil was analyzed for C and N fractions, including total, particulate, microbial biomass, macroaggregate, and mineralizable (Franzluebbers et al., 1999). An adjacent field study with two replications of 0 and 100% endophyte infection was established in 1988-1989 and water infiltration determined in September 1997.

The short-term growth study consisted of 48 experimental units (2.5 kg of soil in 15-cm diam pots) harvested at 8, 20, 36, and 60 weeks of growth. Half of the pots contained a clayey soil and half contained a sandy soil. Within each of the two soils, tillers from 2-year-old endophyte-free and endophyte-infected K-31 tall fescue were grown with balanced fertilizer and watered regularly. Plant growth was measured and soil was analyzed for C and N fractions, including total, particulate, microbial biomass, macroaggregate, and mineralizable, as well as for

microbial diversity with a substrate utilization procedure and fluorescent in situ hybridization.

The short-term decomposition study consisted of 96 experimental units (100 g of soil + 5 g of fresh leaf addition). Leaves were collected from 11-year-old endophyte-free and endophyte-infected K-31 tall fescue pastures in late May and incubated in two different soils (i.e., pastures supporting endophyte-free and -infected tall fescue). Vessels were moistened to 50% water-filled pore space and incubated at 25 EC. Contents of vessels were removed at 0, 1, 2, 4, 8, 16, and 32 days. Soil microbial biomass C, mineralizable C and N, and ergot alkaloids in remaining leaves, water extract, and soil sediment were determined (Hill and Agee, 1994).

Results

Soil organic C and total N in 20-year-old K-31 tall fescue pastures were greater with high endophyte infection (80%) than with low endophyte infection (40%), but only with the high fertilization rate (336-37-139 kg N-P-K Aha⁻¹ Ayr⁻¹) and not with the low fertilization rate (134-15-56 kg N-P-K Aha⁻¹ Ayr⁻¹) (Table 1). Rates of C and N sequestration due to higher endophyte infection would be equivalent to 36 and 163 kg C Aha⁻¹ Ayr⁻¹ and 5 and 12 kg N Aha⁻¹ Ayr⁻¹ under low and high fertilization rates, respectively.

| Table 1. Soil organic C and total N at a depth of 0-20 cm under K-31 tall fescue with low and high endophyte infection. | | | |
|---|-----------|----------|------|
| Management | Endophyte | | |
| | Low | Prob > F | High |
| Soil Organic Carbon (Mg Aha ⁻¹) | | | |
| Low fertilization | 37.2 | 0.71 | 38.0 |
| High fertilization | 38.7 | 0.11 | 42.0 |
| Total Soil Nitrogen (Mg Aha ⁻¹) | | | |
| Low fertilization | 2.25 | 0.48 | 2.34 |
| High fertilization | 2.42 | 0.09 | 2.66 |

Water infiltration in paddocks with 100% endophyte infection (21 cm Ah⁻¹) was greater than in paddocks with 0% endophyte infection (13 cm Ah⁻¹). Soil organic C in these paddocks was not different at sampling in 1997 (23.9 vs 23.7 Mg Aha⁻¹ to a depth of 15 cm under 100 and 0% endophyte infection, respectively). These data suggest that small alterations in soil organic matter might have large impacts on water cycling and potential plant productivity.

The short-term growth study revealed changes in soil organic C pools that were opposite to field studies, suggesting that long-term expression of endophyte effects might possibly be different than short-term effects. There was some indication of greater plant productivity potential with endophyte infection than without (Table 2).

Addition of endophyte-infected tall fescue leaves to soil resulted in lower mineralizable C (660 vs 688 mg Akg⁻¹; $p < 0.01$) and soil microbial biomass C (487 vs 583 mg Akg⁻¹; $p = 0.08$) than addition of

| Table 2. Plant and soil properties from Jesup=tall fescue averaged across 4 sampling dates during 60 weeks of growth without (E-) and with (E+) endophyte infection. | | | |
|--|-----|--------|-----|
| Property | E- | Prob>F | E+ |
| Dry matter production (g Apot ⁻¹) | 31 | 0.10 | 33 |
| Soil organic C (g Akg ⁻¹) | 3.8 | 0.07 | 3.6 |
| Particulate organic C (g Akg ⁻¹) | 1.1 | 0.06 | 1.0 |
| Soil microbial biomass C (mg Akg ⁻¹) | 235 | 0.43 | 226 |
| Mineralizable C (mg Akg ⁻¹ A24 d ⁻¹) | 227 | 0.51 | 218 |
| Macroaggregate C (g Akg ⁻¹) | 1.6 | 0.37 | 1.7 |

endophyte-free leaves. In contrast, the effect of endophyte-infected leaves on mineralizable N (56 vs 19 mg Akg⁻¹; $p = 0.02$) and soil microbial biomass N (70 vs 59 mg Akg⁻¹; $p = 0.08$) was positive compared with endophyte-free

leaves. Ergot alkaloid concentration in leaves declined logarithmically with time during decomposition with an initial increase with time detected in water extracts and a minor accumulation in soil sediment (data not shown). The short-term decomposition study revealed that ergot alkaloids were released from decomposing leaves, but accumulation in soil solution and within the soil matrix may be occurring. In fact, ergot alkaloid concentration was greater ($p < 0.05$) in soil exposed to 10 years of endophyte-infected tall fescue pasture (28 ng Ag^{-1}) than in soil exposed to endophyte-free tall fescue (12 ng Ag^{-1}).

Conclusions

Whether ergot alkaloids in wild-type endophyte-infected tall fescue have a direct or indirect effect on soil organic matter dynamics remains unknown, but the results of these investigations do suggest that soil biochemical transformations are altered by endophyte infection of tall fescue. A field study initiated in 2002 comparing Jesup tall fescue with three different endophyte associations (high endophyte-high alkaloid, high endophyte-low alkaloid, and no endophyte) in a water catchment field design will help us to elucidate mechanisms controlling soil organic matter accumulation and its interactions with nutrient cycling and water quality.

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